

Proliferation of elongate fishes in the deep sea

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It was hypothesized that energetically efficient anguilliform swimming and axial elongation in fishes is favoured in the deep sea and predicted that the degree of elongation of the body form of fishes would increase with depth. An index of fish shape was derived from the relationship between length and mass. This was combined with data on abundance of *c.* 266 fish species from 389 research trawl tows made at depths of between 300 and 2030 m in the north-east Atlantic Ocean. The degree of elongation of the fish increased with depth to *c.* 1250 m before levelling off. The strength of this phenomenon varied between higher level taxa, being most apparent in the Gadiformes and Osmeriformes, and weak or absent in the Perciformes and Selachimorpha. The advantage of efficient elongate body forms may explain why certain taxa such as the grenadiers (Macrouridae) have dominated the deep sea, some have restricted depth ranges, *e.g.* the sharks, skates and rays, and others are almost entirely absent, *e.g.* the flatfishes (Pleuronectiformes).

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Key words: anguilliform; benthopelagic; body shape; fish diversity; swimming efficiency.

INTRODUCTION

The environmental changes that occur from the sea surface to the deep sea represent one of the greatest physical and biological gradients on the planet (Gage & Tyler, 1991), prompting much speculation on trends in physiology, biomass, body size and biodiversity (Rex & Etter, 1998; Herring, 2002; Tittensor *et al.*, 2011). The deep-sea fish assemblages around the world show taxonomic clustering with respect to depth (Snelgrove & Haedrich, 1985; Gordon & Bergstad, 1992; Williams *et al.*, 2001; Powell *et al.*, 2002; Priede *et al.*, 2009; Campbell *et al.*, 2011; Currie *et al.*, 2012). Red fish (Scorpaenidae), ling (Lotidae), hakes (Merluccidae) and argentines (Argentinidae) are found mainly on the upper slopes. Cut-throat eels (Synphobranchidae), spiny eels (Notacanthidae), scabbard fishes (Trichiuridae), deepwater sharks (*e.g.* entrophoridae), skates (Rajidae) and rabbitfishes (Chimaeridae) are found mainly on the mid-slopes. The lower slopes are dominated by the smoothheads (Alepocephalidae), halosaurs (Halosauridae), brotulas (Bithitidae), cusk eels (Ophidiidae) and grenadiers (Macrouridae). The grenadiers and cusk eels extend to abyssal depths in excess of 6000 m, but the very deepest hadal regions of the oceans (>6000 m)

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appear to have been colonized by a single family, the Liparidae (Jamieson *et al.*, 2009). Seamounts and mid-ocean ridges are rather different and tend to be characterized by the presence of roughies (Trachichthyidae), alfonosinos (Berycidae), oreos (Oresomatidae) and cardinal fishes (Apogonidae). Equally important is the notable absence of certain major fish taxa from the deep sea (Merrett & Haedrich, 1997). The tunas and mackerels (Scombridae) and jacks (Carangidae) may temporarily visit the deep sea (Howell *et al.*, 2010), but none dwell there permanently. There are very few flatfish species (Pleuronectiformes) at depths > 1000 m (Jamieson & Yancey, 2012) and no elasmobranchs are reported from waters > 3500 m (Priede *et al.*, 2006).

Metabolic rate has been proposed as a universal driver of form and function in the marine environment (Childress *et al.*, 1980; Childress, 1995; Seibel & Drazen, 2007). Metabolism is reported as low and constrained in the deep sea; interspecific metabolic measurements, either direct whole-animal oxygen-consumption rates (Smith, 1978; Tortes *et al.*, 1979) or indirect measurements of activities of metabolic enzymes (Childress & Somero, 1979; Sullivan & Somero, 1980), show a general pattern of decreasing metabolic activity with increasing depth. The reasons why metabolic rate declines with depth are not immediately clear because it appears not to be an adaptation to the food limitation (Childress, 1995), low temperature or high pressure (Seibel & Drazen, 2007) of the deep sea. If, however, it is considered that the high energy requirements associated with visually orientated predator–prey interactions are contingent upon light, then release from this selective force in the dark deep waters opens the way for more efficient lifestyles and lower metabolic rates to evolve (Childress, 1995; Seibel *et al.*, 2000). Energy saved can be reallocated to growth and reproduction. This may underlie the evolution of a suite of traits in deep-sea fishes including the reduced skeletal density and highly gelatinous muscle tissue of many deep-sea fishes (Pelster, 1997) and, the subject of this study, swimming efficiency and body form.

Body and fin form is strongly linked to swimming performance and efficiency in fishes (Langerhans & Resnick, 2010). Around 10% of fish species swim using their fins as the primary means of locomotion, *e.g.* parrotfishes (Sparidae) use their pectorals and triggerfishes (Balistidae) use their dorsal and anal fins. The other 90% of fish species swim using lateral body undulations running from head to tail (Webb, 1984, 1988; Videler, 1993; Wardle *et al.*, 1995). There are two basic types of axial swimming that are distinguishable on the basis of the pattern of body undulation: anguilliform, as seen in eels, and carangiform, as seen in mackerels. In the anguilliform mode of swimming most of the body is flexible and participates in the propulsive movement with the amplitude of lateral motion from head to tail increasing linearly. In carangiform swimming, the amplitude from head to tail increases as a power function and lateral motion is thus concentrated near the tail (Videler, 1993).

Anguilliform swimming has been theoretically shown to be highly efficient at low swimming speeds (Vorus & Taravella, 2011). This is because it creates circular flow patterns that travel posteriorly with the body wave, thereby generating constant thrust from the body surface (Müller *et al.*, 2001) and minimizing the wake-induced drag (Tytell, 2007; Vorus & Taravella, 2011). Eels have been estimated to be four to six times more efficient at swimming than non-eel-like fishes (van Ginneken *et al.*, 2005). Of special interest is that anguilliform swimming is predicted to become increasingly efficient at higher water viscosities (Borazjani & Sotiropoulos, 2009) and because the viscosity of water increases with hydrostatic pressure and decreases with temperature (Likhachev, 2003), efficiency may increase with depth. Although

the magnitude of increase in water viscosity with depth may be small, there is empirical evidence to show that captive eels swimming at constant rates become more efficient (consume less oxygen) as hydrostatic pressure increases (Sébert *et al.*, 2009). It remains to be tested whether this arises as a physical consequence of increased water viscosity or is a biotic response to hydrostatic pressure. Although most of this recent work is theoretical and the empirical evidence is limited to the study of freshwater eels, it does suggest that anguilliform swimming is more efficient than previously thought and may be of particular functional relevance to deep-sea fishes. Anguilliform swimming is contingent upon an elongated body and if it does indeed offer a selective advantage in the deep sea, it might be expected to see this reflected in the body shape of deep-sea fishes.

Deep-sea fishes range in body shape (Fig. 1) from those that are near-linear, *e.g.* slender snipe eel *Nemichthys scolopaceus* Richardson 1848, to those that are laterally compressed and stocky, *e.g.* blue-mouth red fish *Helicolenus dactylopterus* (Delaroche 1809). Eel-like or elongate fishes in the deep sea have been remarked upon since the earliest explorations (Murray & Hjort, 1912; Marshall, 1979). The elongate rat-tail body plan, characteristic of many deep-sea species, has evolved independently in the Chondrichthyes through the Chimaeriformes and much later in the Osteichthyes through the Macrouridae (Lund & Grogan, 1997; Kriwet & Hecht, 2008). Species belonging to these taxa have long-pointed tails with little or no caudal fin, large heads, and tend to be scavengers and predators of invertebrates. The eels have also proliferated in the deep sea; there are nine families (Nelson, 1994) and some such as Kaup's arrowtooth eel *Synphobranchius kaupi* Johnson 1862 are among the numerically dominant species of the deepwater fish communities of the North Atlantic Ocean (Haedrich & Merrett, 1990; Gordon & Mauchline, 1996).

To test the hypothesis that body forms become increasingly elongate and prevalent with increasing depth, a metric of fish shape is needed that can be generated for all species. For fishes, such a metric is readily obtained from the relationship between mass (M) and length (L) of a species: $M = aL^b$. This relationship is described by two parameters a and b , where a , the intercept, captures the axial dimensionality of the species and b , an exponent, captures the relative change in mass for an increase in length. If a fish grows without changing its shape or density then it exhibits isometric growth, *i.e.* its mass is proportional to its length. The modelled relationship between length and mass will be an isometric growth of $b = 3$. If $b > 3$, the fish increases proportionally more in mass than it does in length, which is termed positive allometric growth. If $b < 3$, the opposite applies and this is termed negative allometric growth. In combination, the a and b parameters can be configured to generate an index of shape of the fish, termed the 'form function' by Froese (2006). The form function is derived as such: the slope (S) of $\log_{10} a$ and b is used to estimate for a given mass and length relationship the value that coefficient a would have if exponent b was 3 (isometric). Consequently, low form function values correspond to elongate shape and high values to a more cubic or spherical shape.

This metric (form function) of fish shape was used in combination with species abundance data from deepwater scientific trawl surveys to assess how the overall form of the fish community changes with depth. This enabled testing of the hypothesis that in deep-sea fishes, body shape becomes more elongate with depth. This may

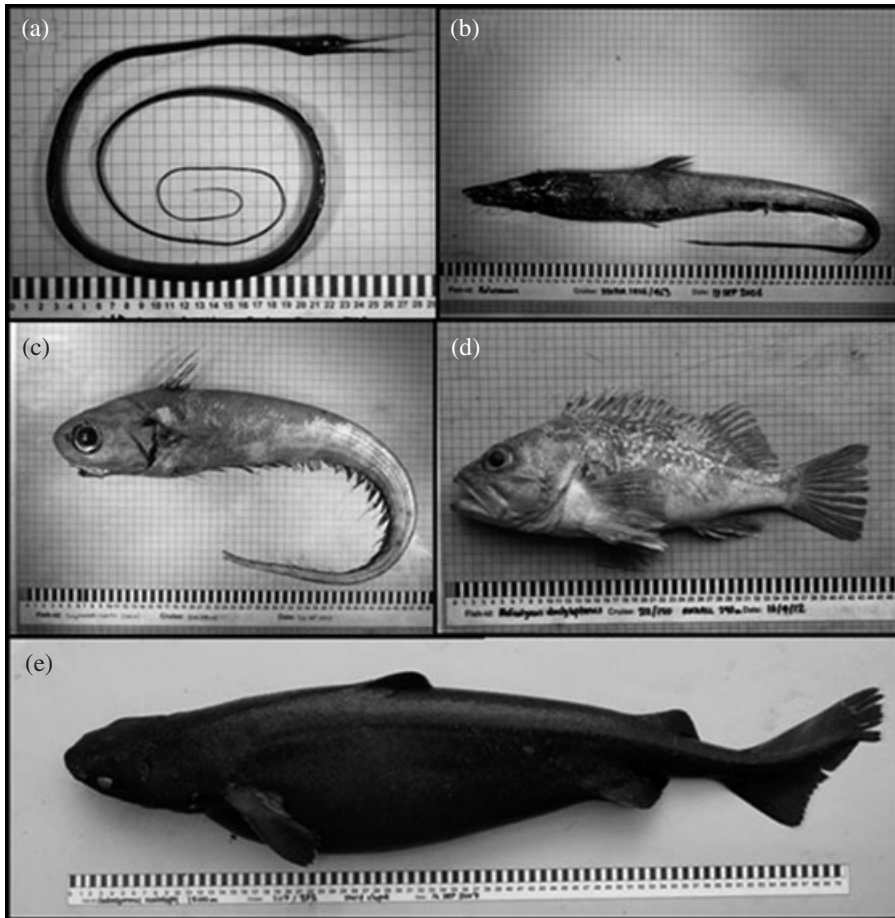


FIG. 1. Representative species of deepwater fishes illustrating diversity in the form factor ($a_{3,0}$): (a) extremely elongate species *Nemichthys scolopaceus* ($a_{3,0} = 0.0007$), (b) a highly elongate species with the rat tail body form *Halosaurus machrochir* ($a_{3,0} = 0.0017$), (c) an elongate species *Coryphaenoides rupestris* ($a_{3,0} = 0.003$), (d) a non-elongate species *Helicolenus dactylopterus* ($a_{3,0} = 0.016$) and (e) *Centroscymnus coelolepis* ($a_{3,0} = 0.004$).

then explain some of the higher taxonomic structures observed in the demersal fish communities of the deep seas.

MATERIALS AND METHODS

Scientific dual-warped bottom trawls with rock-hopper ground gear (Neat *et al.*, 2010) were carried out at 389 sites along the deepwater slopes and seamounts of the Rockall Trough to the west of Scotland (Fig. 2) by the M.R.V. *Scotia*. Surveys were carried out between the years 1998 and 2012 at depths of between 300 and 2030 m, but mainly at four depth strata: 500, 1000, 1500 and 1800 m. A sensor (HP Centi, Star Oddi Marine Device Mfg; www.star-oddi.com) attached to the net recorded the temperature and pressure on hauls since 2005 ($n = 271$). Trawl duration was between 30 min and 2 h at a towing speed of 3.5 knots (6.5 km h^{-1}). This is equivalent to 1.8 m s^{-1} , which is considered effective for catching most

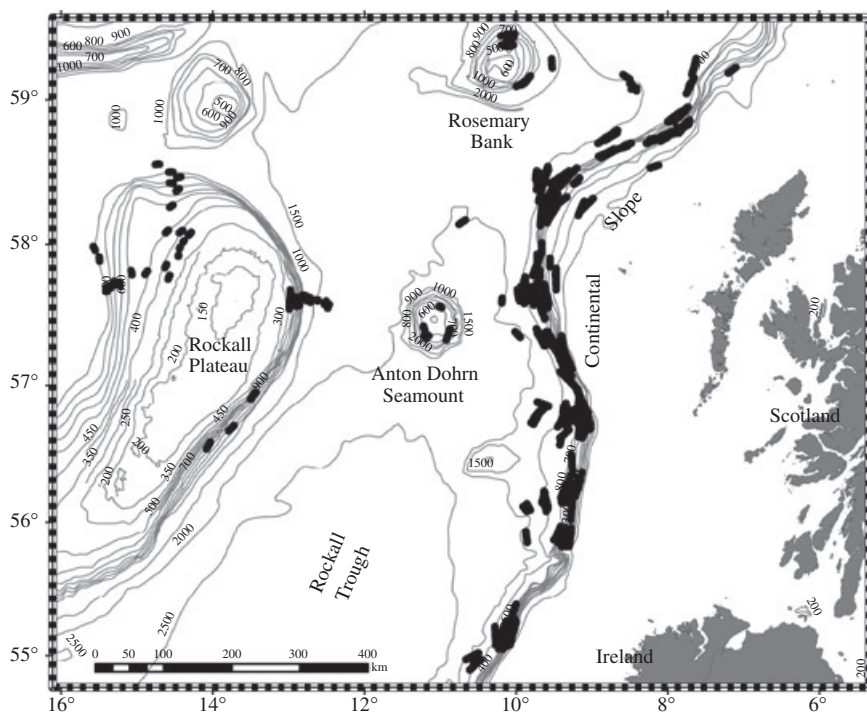


FIG. 2. Map of trawl sampling stations (—). Bathymetric contours (—) and depths in metres are shown.

species of demersal fishes. The trawl gear does not sample every fish that comes into its path as some escape or go under the ground gear. There is no evidence, however, that the gear was selectively biased towards certain species (Neat *et al.*, 2010) and because the mesh size in the codend was fine (20 mm), the catch can be considered representative of all but the very smallest (<20 mm) of the demersal fish community.

Fishes were identified to species and measured. The database comprised records of 842 468 individuals from *c.* 266 taxa. A sample of individuals of each species was weighed to ± 1 g using a regularly calibrated sea-going balance. From these data, significant $\log_{10} L_T$ (total length) and $\log_{10} M$ relationships were calculated for 98 species (Table AI) accounting for 98.6% of all fishes recorded. The remaining 1.4% of individuals were mainly species too rare to acquire sufficient data to generate a significant regression. The form factor ($a_{3.0}$) (Froese, 2006) was derived for each of the 98 species using parameters *a* and *b* from the equation describing the relationship between L_T and M and calculated as: $a_{3.0} = 10^{\log_{10} a - S(b-3)}$, where *S* is the slope of the regression of $\log_{10} a$ and *b*.

The mean $a_{3.0}$ for each haul was plotted against depth (*D*) and a linear model was fitted to this relationship: $\log_{10} a_{3.0}$ function of *D*.

To investigate potential phylogenetic bias, analyses were made of $a_{3.0}$ in relation to the mean depth of occurrence of each species and within the main taxa for which data were available, *e.g.* Perciformes, Gadiformes, Osmeriformes and Selacimorphes.

RESULTS

There was a highly significant declining trend ($F_{1,387} = 540.6$, adjusted $r^2 = 0.582$, $P < 0.001$) in the mean $a_{3.0}$ value of the fish community with *D*

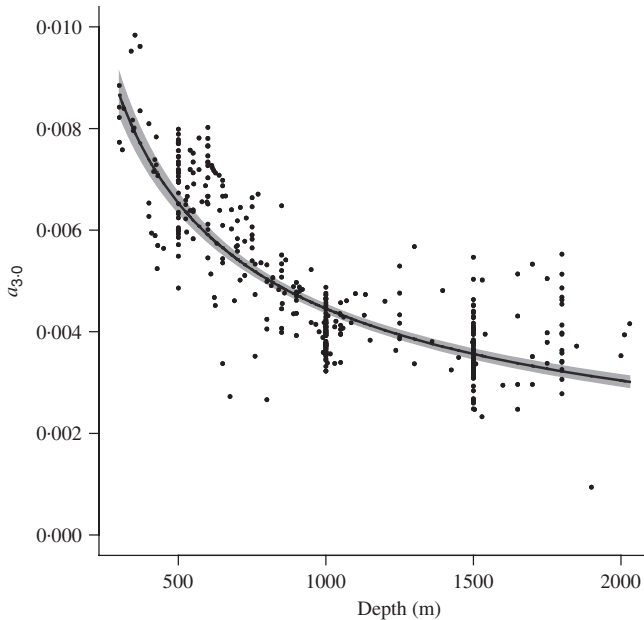


FIG. 3. Mean form factor value ($a_{3.0}$) per haul at depth. Trend line represents fitted values of a linear model ($P < 0.001$) with 95% c.i. (—). The curve was fitted by: $y = e^{-0.683 \ln x - 0.29}$.

(Fig. 3). The trend began to level off at depths > 1250 m and had flattened at depths > 1500 m. The trend mirrored seabed temperature even more closely than depth (Fig. 4), although lack of temperature data for all hauls in the study precluded a formal analysis. Analysis of the trend within the main taxa reveals it to be most apparent within the Gadiformes and Osmeriformes (Fig. 5), whereas weaker in, or absent from, the Perciformes, Anguilliformes, Notacanthiformes, Pleuronectiformes and Selachimorpha (Fig. 6).

DISCUSSION

Given that only M and L_T data were available, Froese's (2006) $a_{3.0}$ served as a useful proxy of fish shape. The average body shape of the fish community elongated with depth, with the fastest rate of change occurring between 300 and *c.* 1250 m. At depths > 1250 m the rate of change slowed and it appeared to have levelled off after 1500 m. Although sampling was done only to a maximum depth of 2030 m and the majority of the deep-sea fishes lie at depths greater than this, the fact that the relationship had levelled off well above 2000 m suggests that the degree of elongation is unlikely to change further. This presumably reflects both the geometry of shape change as $a_{3.0}$ approaches a minimum value and the fact that the greatest environmental change (*e.g.* temperature, food availability, light and pressure) occurs in the upper 1500 m. This study can be considered broadly representative of deep-ocean fish communities because most of the families of fish sampled have sub-polar global distributions (Nelson, 1994). Furthermore, although sampling was restricted

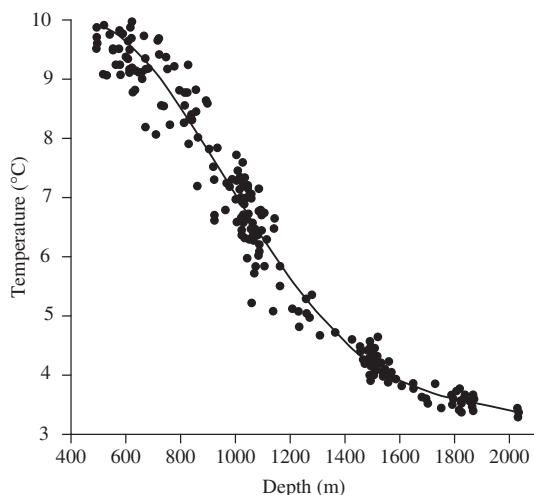


FIG. 4. Temperature and depth data collected from the sensor on the net with polynomial fit. The curve was fitted by: $y = 4E-12x^4 + 2E-08x^3 - 4E-05x^2 + 0.0279x + 4.5061$.

to areas where a bottom trawl could be deployed (reasonably smooth seabed) this did include seamounts and offshore banks as well as the continental slope. The data are therefore representative of various types of deep-sea ecosystems and habitats.

In the deep sea, sustained high-speed pursuit or escape swimming has little benefit as there is insufficient light to hunt prey or find refuge (Childress, 1995; Seibel *et al.*, 2000). With the release from the need for high-performance swimming, deep-sea fishes have evolved adaptations that reduce energy costs and allow saved energy to be channelled into growth and reproduction. Many deep-sea species have reduced

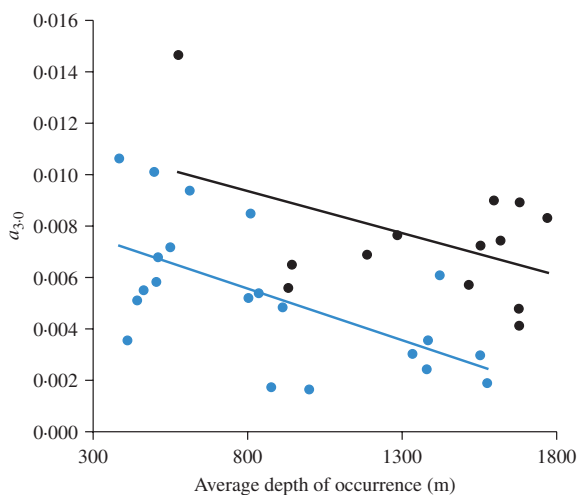


FIG. 5. Variation in form factor ($a_{3,0}$) with mean depth for species of Gadiformes (●; $y = -3E-06x + 0.012$; $r^2 = 0.37$) and Osmeriformes (●; $y = -4E-06x + 0.012$; $r^2 = 0.21$).

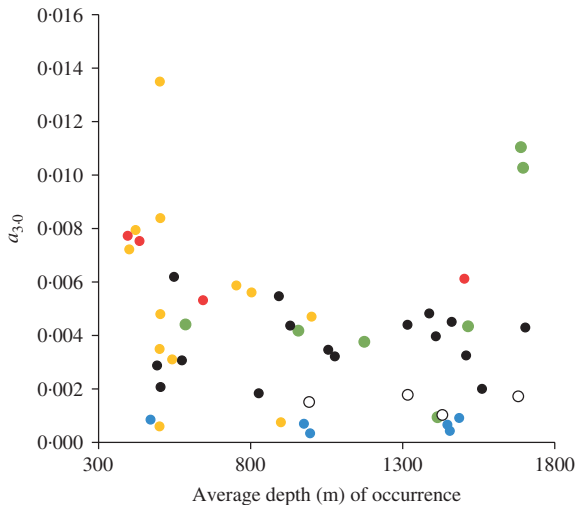


FIG. 6. Variation in form factor ($a_{3.0}$) with mean depth for species of Perciformes (●), Anguilliformes (●), Chimaeriformes (●), Notacanthiformes (○), Selachimorpha (●) and Pleuronectiformes (●).

skeletal density and highly gelatinous muscle tissue (Pelster, 1997) and some species have evolved extensible or snaggletooth jaws that increase predatory efficiency without the need for fast acceleration and power swimming. The anguilliform mode of swimming, being especially efficient at slow speeds (van Ginneken *et al.*, 2005; Tytell *et al.*, 2010; Vorus & Taravella, 2011) and potentially increasing in efficiency with depth (Borazjani & Sotiropoulos, 2009; Sébert *et al.*, 2009), may be favoured in deep-ocean conditions. An analogous situation is found in cephalopods; shallow water squids swim at high speed using jet propulsion, whereas deep-water squids swim using their fins at lower speeds, but with greater efficiency (Seibel *et al.*, 2000). In this study, the use of $a_{3.0}$ allowed body shape to be readily quantifiable across species to reveal a gradual increase in elongation with depth.

Potentially confounding effects of phylogeny were not explicitly controlled for in the community-scale analysis owing to ambiguities over the phylogenetic relationships of all species. Importantly, however, the trend persisted independently within the phylogenetically distant Gadiformes and Osmeriformes, suggesting that the result is not unduly biased by phylogeny. Furthermore, as the data used was derived from 98 species across 45 families and from both classes of fishes (Chondrichthyes and Osteichthyes) it was broadly representative of deep-sea demersal fishes. A recent study on deep-sea fish life histories (Drazen & Haedrich, 2012) also concluded that depth-related environmental gradients explained much of the variation rather than phylogeny.

Species from the family Macrouridae were the most numerous and they have elongate and highly tapered body forms. The reason for their tapered body form as opposed to uniformly elongate is not known and this is an interesting question for biophysical studies to address. Anguilliforms are numerous and diverse in the deep ocean and were also well represented in these data, *e.g.* *S. kaupii*. It has recently been demonstrated that anguilliforms evolved in the deep oceans prior to invading shallow

and freshwater habitats (Inoue *et al.*, 2010), further supporting the idea that anguilliform swimming may be associated with adaptation to the deep sea. The swimming style of the freshwater eel *Anguilla anguilla* (L. 1758) may also explain how it is able to undertake such extraordinary long migrations at depths of >600 m (Aarestrup *et al.*, 2009). The black-scabbard fish *Aphanopus carbo* Lowe 1839 was also abundant in the samples and is suspected of undertaking extensive migrations and is highly elongate (Figueiredo *et al.*, 2003). An elongated body shape may also confer further advantages: the presence of continuous fins along the body facilitates backward swimming and rapid braking, which may be of benefit to a fish that relies on finding prey in the dark (Videler, 1993). In the shallower realms of the oceans, elongate fishes are often found in association with burrows (*e.g.* the red band fish *Cepola rubescens* L. 1758), holes or complex structural habitat. Such behaviour–habitat associations have not to date been reported for deep-sea species and thus is unlikely to be an important factor in explaining the pattern observed in this study.

The elongation in fishes probably happens through either an increase in the number of vertebrae or an increase in relative length of the vertebrae (Ward & Brainerd, 2007). *hox* genes (that among many roles, regulate axial development) may be the underlying reason for axial diversity in fishes and there are some interesting comparative patterns in the *hox* gene number in fishes, ranging from a reduced complement in sharks (King *et al.*, 2011) to full duplication in teleosts (Kuraka & Meyer, 2009). Such developmental mechanisms and constraints could be important in explaining the pattern observed in the data.

Of those non-elongate species found only in the upper slopes of the deep sea, some may be developmentally constrained in their potential to elongate, which may explain their absence from deeper realms. The laterally compressed Perciformes showed no apparent trend in elongation with depth. The highly fusiform body of the Scorpaenidae (red fishes or scorpion fishes) may be another example. The characteristically flattened Pleuronectiformes (flatfishes) are almost entirely absent from the deep sea, despite the deep-sea bed being predominantly sedimentary and apparently otherwise suitable for them. The chondrichthyan body structure presents a particular challenge to explain. The deepwater sharks (Selachimorpha), while noticeably more elongate than their shallow-water pelagic counterparts, showed no tendency to further elongate with depth, suggesting that they may be constrained by their fusiform body structure. This study suggests that sharks are rarely encountered at depths beyond 2000 m and Priede *et al.* (2006) present evidence that they are entirely absent at depths >3500 m. Priede *et al.* (2006) ascribed this to the high energy demands imposed by an oil-rich buoyant liver. Recently, Laxson *et al.* (2011) hypothesized that a pressure-induced biochemical constraint to urea excretion might play a role in setting the bathyal zone as limit to sharks. This study suggests that the fusiform body structure of sharks may act as a further constraint to their swimming efficiency and thus preclude them from the deepest realms. The skates and rays (Rajiformes) have a flattened body plan and swim by undulating their greatly expanded pectoral fins (Daniel, 1988). Nevertheless, none are reported deeper than 3900 m (Froese & Pauly, 2013). The mode of swimming of Chimaeriformes is different; they are highly tapered elongate fishes that use their pectoral fins in swimming. Pectoral fin swimming at slow speeds has been shown to be highly efficient (Webb, 1984), suggesting that swimming efficiency alone cannot explain why they are only found to a maximum depth of 3000 m (Froese & Pauly, 2013).

Not all deep-sea fishes are eel-like. Those that are not, however, such as the orange roughy *Hoplostethus atlanticus* Collett 1889 or alfonsoins *Beryx* spp., are associated with steep sloped and physically dynamic seamount environments where the energy flux is greater than the deep seas in general. Other non-eel-like species such as the eratidae (deep sea anglerfish) tend to be rare ones that are sit-and-wait predators. For such species, swimming has become effectively redundant and they have ballooned in shape to accommodate large prey. Curiously, the deepest of species, the Liparidae, are tadpole-shaped (large heads and elongate tails). This may reflect a compromise between swimming efficiency and the need to gorge at rare food-fall events that are the main source of energy in the hadal zones (Jamieson *et al.*, 2009). Being ecological or behavioural exceptions, such cases reinforce the need for the general prevalence of elongate fishes in the deep sea. While there are numerous adaptive traits of deep-sea fishes, the selective advantages of more efficient elongate body forms may be one important factor that explains why certain taxa, such as the grenadiers (Macrouridae), have dominated the deep sea, some have restricted depth ranges, *e.g.* the sharks, skates and rays, and others are almost entirely absent, *e.g.* the Pleuronectiformes.

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APPENDIX

TABLE AI. Details and equation parameters of total length (L_T) and mass (M) relationships for species of deepwater fishes used in the analysis presented in Fig. 3. Species sorted in the order of form factor ($a_{3.0}$) from low (eel-like) to high (fusiform). Additional information is also given on minimum and maximum L_T , M and data on the depth of occurrence (D)

Family	Species	n	a	β	r^2	$a_{3.0}$	Minimum L_T (cm)	Maximum L_T (cm)	Maximum M (g)	Mean D (m)	Minimum D (m)	Maximum D (m)
Derichthyidae	<i>Nessorhamphus inglofianus</i>	11	$8.00E^{-05}$	3.507	0.972	0.00039	37	54	96	995	550	1500
Trachipteridae	<i>Trachipterus arcticus</i>	22	$5.00E^{-05}$	3.699	0.73	0.00044	112	218	20 000	1009	550	1800
Serrivomeridae	<i>Serrivomer beani</i>	49	0.00001	4.239	0.595	0.00048	41	81	737	1455	570	2030
Trichiuridae	<i>Aphanopus carbo</i>	628	0.00011	3.558	0.918	0.00063	61	117	2254	917	500	2012
Synphobranchidae	<i>Synphobranchius kaupii</i>	369	$2.00E^{-04}$	3.397	0.97	0.00069	16	73	470	1448	430	2030
Nemichthyidae	<i>Nemichthys scolopaceus</i>	13	0.1803	1.229	0.133	0.00071	77	110	86	975	450	1800
Zoarcidae	<i>Lycodon flagellacaudum</i>	16	0.00073	3.022	0.847	0.00078	12	23	22	1370	900	1800
Congridae	<i>Conger conger</i>	79	$1.00E^{-04}$	3.685	0.973	0.00085	35	163	12 750	470	300	780
Nettastomatidae	<i>Venifica proboscidea</i>	7	0.00001	4.453	0.72	0.00094	84	105	375	1488	1000	1650
Rhinochimaeridae	<i>Rhinochimaera atlantica</i>	39	0.00019	3.521	0.987	0.00097	56	139	6340	1414	950	1800
Notacanthidae	<i>Polyacanthodonotus rissoanus</i>	57	0.01466	2.155	0.639	0.00104	24	53	119	1434	500	2030
Notacanthidae	<i>Notacanthus bonapartei</i>	112	0.00094	3.155	0.971	0.00153	18	53	298	992	500	1800
Macrouridae	<i>Macrourus berglax</i>	20	0.00201	2.938	0.972	0.00166	86	156	5576	1000	1000	1000
Lotidae	<i>Molva dypterygia</i>	243	0.00037	3.493	0.942	0.00173	42	135	10 700	877	400	1500
Halosauridae	<i>Halosaurusis macrochir</i>	32	0.00557	2.628	0.699	0.00174	55	74	452	1681	800	2030
Notacanthidae	<i>Notacanthus chemnitzii</i>	134	0.00063	3.337	0.983	0.00181	20	113	5498	1319	622	2000
Centrophoridae	<i>Deania calceus</i>	301	$3.00E^{-04}$	3.58	0.922	0.00184	64	111	8130	825	430	1504
Myxiniidae	<i>Myxine ios</i>	55	0.05608	1.909	0.539	0.00185	14	53	442	1343	850	1500
Macrouridae	<i>Coryphaenoides mediterranea</i>	354	0.00276	2.876	0.984	0.00187	11	99	1856	1576	800	2030
Sylliorhinidae	<i>Apristurus manis</i>	26	0.00036	3.551	0.939	0.00202	46	96	3180	1562	1500	1800
Hexanchidae	<i>Hexanchus griseus</i>	24	$4.00E^{-04}$	3.527	0.987	0.00208	71	246	130 200	504	400	780
Macrouridae	<i>Trachyrhynchus murrayi</i>	653	0.00458	2.8	0.834	0.00245	9	62	727	1382	700	1850
Sylliorhinidae	<i>Galeus melastomus</i>	332	0.00213	3.097	0.952	0.00288	21	77	1542	492	300	1500
Macrouridae	<i>Coryphaenoides guentheri</i>	331	0.01526	2.477	0.929	0.00297	7	58	278	1553	500	2030
Macrouridae	<i>Coryphaenoides rupestris</i>	654	0.00629	2.764	0.949	0.00301	4	104	2130	1335	500	2030
Dalatidae	<i>Scymnorhinus (Dalatias) licha</i>	23	0.00087	3.404	0.952	0.00308	46	147	21 500	573	500	1500

TABLE AI. Continued

Family	Species	<i>n</i>	<i>a</i>	β	<i>r</i> ²	<i>a</i> _{3.0}	Minimum <i>L</i> _T (cm)	Maximum <i>L</i> _T (cm)	Maximum <i>M</i> (g)	Mean <i>D</i> (m)	Minimum <i>D</i> (m)	Maximum <i>D</i> (m)
Zoarcidae	<i>Lycodes atlanticus</i>	76	0.00134	3.27	0.971	0.00312	8	56	735	1319	540	2012
Scyllorhinidae	<i>Apristurus laurussonii</i>	19	0.00293	3.031	0.996	0.00323	11	75	1320	1076	815	1500
Scyllorhinidae	<i>Apristurus melanoasper</i>	106	0.00253	3.082	0.985	0.00327	20	75	1303	1509	1000	1850
Scyllorhinidae	<i>Galeus murinus</i>	19	0.00187	3.199	0.987	0.00348	16	45	354	1056	500	1500
Zoarcidae	<i>Melanostigma atlanticum</i>	24	0.00388	2.968	0.796	0.00351	8	15	22	940	500	1800
Macrouridae	<i>Coelorhynchus labiatus</i>	419	0.00948	2.684	0.975	0.00353	4	42	276	1385	700	1850
Macrouridae	<i>Malacocephalus laevis</i>	75	0.00393	2.966	0.93	0.00353	21	62	762	413	300	864
Chimaeridae	<i>Chimaera opalescence</i>	47	0.00328	3.044	0.984	0.00376	18	93	3204	1174	725	1650
Somniosidae	<i>Centroscymnus coelolepis</i>	213	0.00081	3.51	0.95	0.00399	31	115	17 100	1410	709	1800
Alepocephalidae	<i>Centrocara macroptera</i>	17	0.00216	3.207	0.968	0.00413	20	44	439	1678	800	1800
Chimaeridae	<i>Hydrolagus affinis</i>	64	0.00242	3.177	0.976	0.00421	17	49	624	956	530	1504
Scyllorhinidae	<i>Apristurus microps</i>	53	0.00355	3.061	0.987	0.00430	17	70	1556	1704	800	2030
Rhinochimaeridae	<i>Hariootta raleighana</i>	145	0.00641	2.877	0.943	0.00436	31	81	2174	1516	800	2030
Somniosidae	<i>Centroscymnus crepidater</i>	976	0.00274	3.15	0.976	0.00438	24	88	4285	931	528	1800
Etmopteridae	<i>Centroscyllium fabricii</i>	425	0.00254	3.176	0.965	0.00440	15	86	4940	1316	840	1750
Chimaeridae	<i>Chimaera monstrosa</i>	218	0.00465	2.985	0.991	0.00444	8	85	2198	585	300	1800
Scyllorhinidae	<i>Apristurus aphyodes</i>	268	0.01032	2.736	0.888	0.00452	28	79	1340	1462	850	1800
Bythitidae	<i>Cataetys laticeps</i>	199	0.00153	3.361	0.984	0.00473	13	101	6570	1517	1000	2000
Alepocephalidae	<i>Xenodermichthys copei</i>	60	0.01794	2.578	0.966	0.00479	6	19	40	944	500	2000
Gempylidae	<i>Nesiarchus nasutus</i>	6	0.0269	2.45	0.752	0.00482	69	82	1412	727	500	1050
Etmopteridae	<i>Etmopterus princeps</i>	323	0.00289	3.164	0.991	0.00483	16	79	3548	1389	800	1800
Macrouridae	<i>Nezumia aequalis</i>	255	0.00694	2.885	0.839	0.00484	9	26	107	913	500	1750
Rajidae	<i>Brevitaja caerulea</i>	6	0.00605	2.931	0.689	0.00488	29	37	212	1229	622	1900
Lotidae	<i>Molva molva</i>	259	0.00408	3.072	0.992	0.00511	20	131	16 300	442	300	900
Moridae	<i>Halargyreus johnsonii</i>	129	0.00455	3.042	0.928	0.00519	9	36	301	802	500	1800
Chlorophthalmidae	<i>Bathypterois dubius</i>	56	0.00367	3.116	0.961	0.00527	10	25	72	1466	750	1800
Pluronectidae	<i>Glyptocephalus cynoglossus</i>	82	0.00224	3.277	0.963	0.00533	20	43	601	643	300	1500
Moridae	<i>Leptidion eques</i>	798	0.00187	3.338	0.978	0.00538	10	37	396	834	450	1500

TABLE AI. Continued

Family	Species	<i>n</i>	<i>a</i>	β	r^2	$a_{3.0}$	Minimum L_T (cm)	Maximum L_T (cm)	Maximum <i>M</i> (g)	Mean <i>D</i> (m)	Minimum <i>D</i> (m)	Maximum <i>D</i> (m)
Centrophoridae	<i>Centrophorus squamosus</i>	129	0.00493	3.033	0.784	0.00547	84	125	18 600	893	500	1900
Gadidae	<i>Micromesistius putassou</i>	5822	0.01072	2.787	0.945	0.00551	9	41	422	465	300	1800
Searsiidae	<i>Holtbyrnia macrops</i>	8	0.00417	3.094	0.946	0.00559	21	33	183	1516	910	2012
Ophidiidae	<i>Spectrunculus grandis</i>	74	0.00452	3.071	0.871	0.00564	36	58	1278	1809	800	2030
Searsiidae	<i>Holtbyrnia anomala</i>	19	0.00564	3.004	0.905	0.00571	16	31	177	1680	800	2012
Macrouridae	<i>Coelorhynchus coelorhynchus</i>	218	0.009	2.861	0.99	0.00583	8	41	329	504	300	1000
Melanonidae	<i>Melanonus zugmayeri</i>	9	0.01205	2.77	0.966	0.00587	15	24	80	978	750	1800
Pleuronectidae	<i>Reinhardtius hippoglossoides</i>	207	0.00144	3.462	0.97	0.00611	40	97	8200	1503	1500	1529
Moridae	<i>Antimora rostrata</i>	218	0.00323	3.204	0.988	0.00611	8	64	2194	1421	592	2030
Etmopteridae	<i>Etmopterus spinax</i>	523	0.04454	2.37	0.744	0.00621	4	58	1046	548	340	1050
Rajidae	<i>Amblyraja jenseni</i>	16	0.00315	3.225	0.987	0.00637	21	99	8435	1663	1500	2030
Alepocephalidae	<i>Alepocephalus bairdii</i>	450	0.00488	3.092	0.994	0.00651	4	91	5200	1186	500	2012
Merlucciidae	<i>Merluccius merluccius</i>	606	0.00637	3.019	0.995	0.00676	9	105	8910	511	300	850
Alepocephalidae	<i>Conocara murrayi</i>	10	0.00166	3.456	0.988	0.00691	20	45	846	1621	800	2030
Rajidae	<i>Rajella fyllae</i>	28	0.03387	2.492	0.909	0.00692	18	53	732	991	500	1500
Gadidae	<i>Phycis blennoides</i>	249	0.00515	3.106	0.988	0.00717	12	79	6700	549	300	1500
Argentinidae	<i>Argentina silus</i>	658	0.0034	3.241	0.987	0.00722	13	48	860	576	300	1086
Bramidae	<i>Brama brama</i>	12	0.00108	3.608	0.948	0.00723	35	61	2860	652	400	1800
Alepocephalidae	<i>Alepocephalus agassizi</i>	160	0.00499	3.128	0.938	0.00745	18	82	5262	1771	800	2030
Scophthalmidae	<i>Lepidorhombus boscii</i>	66	0.00869	2.955	0.983	0.00755	13	35	340	434	300	1000
Bathylagidae	<i>Bathylagus euryops</i>	9	0.01807	2.725	0.897	0.00765	9	18	65	1554	750	2030
Scophthalmidae	<i>Lepidorhombus whiffiagonis</i>	35	0.01556	2.777	0.966	0.00775	17	46	578	395	300	1000
Centrolophidae	<i>Schedocephalus medusaphagus</i>	15	0.00442	3.188	0.958	0.00796	35	61	2222	715	420	1800
Alepocephalidae	<i>Rouleina attrita</i>	85	0.01594	2.792	0.883	0.00832	13	50	1002	1597	800	2030
Centrolophidae	<i>Centrolophus niger</i>	79	0.00592	3.111	0.914	0.00838	34	67	2978	1051	500	1500

TABLE AI. Continued

Family	Species	<i>n</i>	<i>a</i>	β	r^2	<i>a</i> _{3.0}	Minimum <i>L</i> _T (cm)	Maximum <i>L</i> _T (cm)	Maximum <i>M</i> (g)	Mean <i>D</i> (m)	Minimum <i>D</i> (m)	Maximum <i>D</i> (m)
Carangidae	<i>Trachurus trachurus</i>	285	0.00338	3.294	0.97	0.00848	16	41	724	494	300	700
Moridae	<i>Mora moro</i>	280	0.00568	3.128	0.991	0.00848	15	81	3380	810	500	1500
Serranidae	<i>Normichthys operosus</i>	22	0.01361	2.865	0.349	0.00892	10	17	302	1283	760	2030
Alepocephalidae	<i>Alepocephalus rostratus</i>	21	0.01515	2.833	0.857	0.00899	27	42	727	933	700	1500
Lotidae	<i>Brosme brosme</i>	184	0.00599	3.144	0.991	0.00940	19	86	7340	611	300	1500
Gadidae	<i>Trisopterus minutus</i>	832	0.00678	3.128	0.974	0.01012	7	29	269	497	300	600
Chimaeridae	<i>Hydrolagus pallidus</i>	44	0.01964	2.793	0.883	0.01028	41	122	15760	1696	1000	2030
Gadidae	<i>Gadiculus argenteus thori</i>	299	0.00884	3.059	0.958	0.01063	5	15	39	385	300	1800
Chimaeridae	<i>Hydrolagus mirabilis</i>	229	0.02299	2.766	0.872	0.01106	22	119	16180	1690	800	2030
Apogonidae	<i>Epigonus telescopus</i>	77	0.01609	2.944	0.996	0.01351	9	58	2638	744	500	1500
Lophiidae	<i>Lophius piscatorius</i>	1612	0.02057	2.889	0.991	0.01454	5	147	41400	657	300	1500
Alepocephalidae	<i>Bathytroctes microlepis</i>	12	0.18013	2.198	0.871	0.01467	23	27	268	1802	1800	1850
Psychrolutidae	<i>Cottunculus thomsonii</i>	99	0.01577	2.977	0.991	0.01468	5	41	1083	1122	540	1800
Trachichthyidae	<i>Hoplostethus mediterraneus</i>	340	0.01444	3.017	0.806	0.01523	21	30	394	662	500	900
Lophiidae	<i>Lophius budegassa</i>	18	0.03073	2.776	0.994	0.01525	11	71	4809	300	300	300
Scorpaenidae	<i>Sebastes marinus mentella</i>	150	0.02216	2.888	0.774	0.01561	35	55	2196	619	310	1237
Scorpaenidae	<i>Helicolenus dactylopterus</i>	101	0.01467	3.034	0.975	0.01632	18	35	744	469	300	1237
Paraliparidae	<i>Paraliparis bathybius</i>	8	0.00147	3.771	0.911	0.01638	6	11	14	926	580	1800
Trachichthyidae	<i>Hoplostethus atlanticus</i>	982	0.02321	2.928	0.995	0.01853	6	71	6551	1218	525	1800

n, sample size.